

THE EVOLUTION OF DIOECY—CONCLUDING REMARKS

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Since the pioneer work of Darwin on the evolution of sexual systems in plants (Darwin, 1877a, 1877b) no sexual strategy in recent years has attracted as much attention as dioecy. First, a number of population genetic models were developed in the 1970s to trace the evolution of dioecy via different pathways (Lloyd, 1975, 1976, 1979; Ross, 1970, 1978, 1980, 1982; Charlesworth & Charlesworth, 1978a, 1978b). Almost concurrently, field studies highlighted the ecological consequences of dioecy (Bawa & Opler, 1975; Lloyd & Webb, 1977; Wallace & Rundel, 1979; Meagher, 1980, 1981; Bullock & Bawa, 1981). Then a resurgence of interest in the sexual selection theory led to a search for new selective pressures driving the evolution of dioecy (e.g., Willson, 1979). The finding that dioecy is associated with certain pollination and seed-dispersal syndromes further eroded the traditional view that outcrossing is the main selective force in the evolution of dioecy (Bawa & Opler, 1975; Bawa, 1980a; Givnish, 1980; Beach, 1981; but see Thomson & Barrett, 1981; Lloyd, 1982; for a balanced review, see Charnov, 1982). Here, I briefly consider the major unresolved problems in the evolution of dioecy, including some already discussed at length by the contributors to this symposium.

First, a fundamental problem concerns the extent to which sex expression in dioecious species is constant. Freeman et al. (this symposium) document in detail substantial sex reversals in *Atriplex canescens*. On the other extreme the dioecious lily, *Chamaelirium luteum*, studied by Meagher (this symposium) exhibits no change in sex expression. Furthermore, the two sexes in *C. luteum* show remarkable ecological divergence. Sexual dimorphism in many other dioecious species is also pronounced (Lloyd & Webb, 1977; Bawa, 1980b; Bawa et al., 1982; Bullock & Bawa, 1981; Bullock, 1982; Bullock et al., 1983). If indeed there is no constancy in sex expression, then we need models to explain how sex-linked divergence in morphological, behavioral, physiological, and biochemical traits might have evolved. Freeman et al. (1980, this symposium)

mention many other species that presumably change sex, but as pointed out by Lloyd and Bawa (1984), patterns of gender modification in plants are varied and complex. In order to understand the origin of these complex patterns and their adaptive significance, it is necessary to distinguish, for example, extremes such as "sex choosers" (e.g., *Arisaema triphyllum*) and "sex adjustors" (e.g., many dioecious species, see Lloyd & Bawa, 1984). Only a precise quantitative description of gender may allow the resolution of various patterns of gender modification. For many species that are assumed to change sex, such information is simply not available (Lloyd & Bawa, 1984).

Second, the study of evolutionary pathways to dioecism remains an area of major importance. Dioecism has been presumed to have evolved via five distinct routes directly from hermaphroditism and via androdioecy, gynodioecy, monoeecy, and heterostyly (Bawa, 1980a; Ross, 1982). It is not known if the ecological pressures favoring the evolution of dioecy are the same in each pathway. However, the population genetic models for almost all pathways assume selective pressure against inbreeding as the major driving force (Lloyd, 1982; Ross, 1982 and references therein). Field studies for specific taxa are badly needed to test the models. Another major problem in the understanding of evolutionary pathways is the uncertainty about the frequency with which dioecy has evolved directly from hermaphroditism or via androdioecy. In fact, the evolution and occurrence of androdioecy itself has been questioned (Charlesworth & Charlesworth, 1978a, 1978b, pers. comm.; and see Haber & Bawa, this symposium). Systems such as those in *Actinidia chinensis* (Schmid, 1978), *Saurauia* spp. (Haber & Bawa, this symposium) and *Solanum* spp. (Anderson, 1979) may prove to be useful in the search for general models for the evolution of dioecism via androdioecy.

Third, the importance of selection against inbreeding depression (see e.g., Willson, 1979; Bawa, 1980a, 1982a; Givnish, 1980, 1982; Thomson & Barrett, 1981; Beach, 1981; Char-

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nov, 1982; Lloyd, 1982) is, perhaps, the most outstanding of the unresolved issues in the evolution of dioecy because its resolution has the potential to fundamentally alter our overall view of the evolution of sexual systems in plants (Willson, 1979; Bawa & Beach, 1981).

Fourth, explanations for the recently discovered "ecological correlates" of dioecy (Bawa & Opler, 1975; Bawa, 1980a; Givnish, 1980) need to be empirically examined. Divergent opinions have been expressed to account for the association between dioecy and pollination by small bees or generalist insects and that between dioecy and fleshy fruits (Bawa & Opler, 1975; Bawa, 1980a; Beach, 1981; Givnish, 1980, 1982; Charnov, 1982; Lloyd, 1982; see also Bawa, 1982b; Herrera, 1982). In particular, for species pollinated by small bees or generalist insects, we need to know a) if an increase in male reproductive expenditure results in a disproportionate increase in male fitness (Bawa, 1980a; Beach, 1981), and b) if such species are particularly vulnerable to selfing or limited pollen dispersal and if the advantage of dioecy is that it results in outcrossing (Lloyd, 1982). Similarly in species with fleshy fruits dispersed by specialized frugivores, we need to know if an increase in investment in seed and fruit crops results in a disproportionate gain in fitness via enhanced seed dispersal (Bawa, 1980a, 1982; Givnish, 1980; Charnov, 1982; Herrera, 1982; Lloyd, 1982).

Fifth, the origin and evolution of sexual dimorphism—the morphological, physiological, biochemical, genetical, and ecological differences between sexes—is virtually an unexplored area (Lloyd & Webb, 1977; Wallace & Rundel, 1979; Bawa, 1980b; Meagher, 1980, 1981, 1982, this symposium; Meagher & Antonovics, 1982a, 1982b; Bullock, 1982; Bullock & Bawa, 1981; Bullock et al., 1983). As Meagher points out in his paper above, the study of sexual dimorphism is useful in providing insights into the type of selection that results in divergence as well as the ecological consequences of such divergence.

The differences in resource allocation for various functions in different sexual morphs remains a particularly interesting problem, especially the differences between male-sterile and female-sterile mutants and the hermaphrodites that they may eventually replace. Although it is obvious that the mutants, by the "law of compensation" (Darwin, 1877a), should allocate more resources to male or female functions than the hermaphrodites, we do not know the extent to

which these differences are present when the mutant arises versus the extent to which the differences develop during the evolution of dioecy. Note that if, as argued by Lloyd (1982), the initial differences are not large, sudden gains in male and female reproductive success of the mutants may not be possible. Such gains would be especially difficult to make in the absence of inbreeding depression in the original population of hermaphrodites, a phenomenon required in Bawa's (1980a) and Givnish's (1980) hypotheses. In this context, comparative data on the reproductive ecology of various types of male- and female-sterile mutants that arise in a population are also needed. It is possible, and likely, that of the many types of mutants that arise, only a small fraction with appropriate reproductive traits become established to convert a monomorphic population into a sexually dimorphic population.

Ornduff (1983) has recently questioned the preoccupation of biologists with rare sexual systems such as dioecy. After all, approximately 90% of the angiosperms are estimated to be cosexual (Lloyd, 1982). But in asking why plants are dioecious, in many ways we are trying to determine why the vast majority of flowering plants are cosexual (see e.g., Charnov, 1982; Lloyd, 1982).

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